5.—Endemism in the Western Australian flora at the species level

by J. S. Beard[*]

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Abstract

An analysis is given of endemism in the 5802 recorded species of flowering plants from Western Australia. Within the three floral provinces of the state the percentages of endemism at the species level are: Southwestern 79, Northern 77, Eremaean 45. The equivalent percentages for the whole flora of each province when distribution outside the state of Western Australia is taken into account are 86, 30 and 62. Data on constituent families and genera are tabulated.

The distribution of the Australian flora was analysed by Burbidge (1960) at the generic level and it was shown that of the 462 genera represented in the Southwestern Botanical Province of Western Australia 111 are restricted thereto. No similar figures at the species level have been presented in recent years, and in the absence of a published critical Flora of Western Australia it is not easy to do so.

Locality data included by Beard (1965) in the *Descriptive Catalogue of West Australian Plants* afford however a useful basis for calculations. The catalogue lists all the known published species of flowering plants believed to be valid and native to Western Australia to the number of 5312, omitting the grasses and sedges. The distribution of each species is shown in terms of the botanical provinces and districts of Gardner and Bennetts (1956). Similar data on the Gramineae are available in Gardner (1952) where there are 278 native species, and data on 212 species of Cyperaceae have been separately compiled on the basis of those species listed in Gardner (1930).

The range of most species is still imperfectly known, but on the basis of existing knowledge the following figures relate to species distribution within Western Australia itself.

Northern Province only	1117	species
Northern and Eremaean	263	
Northern and Southwestern	22	
All provinces	43	
Total Northern	1445	species
Eremaean Province only	811	species
Northern and Eremaean	263	
Southwestern and Eremaean	705	
All provinces	43	
Total Eremaean	1822	species
Southwestern Province only	2841	species
Southwestern and Eremaean	705	
Northern and Southwestern	22	
All provinces	43	
Total Southwestern	3611	species
TOTAL ALL SPECIES	5802	

As mentioned above, these figures relate only to the distribution within the state of Western Australia as a political rather than a phytogeographical unit. The Northern and Eremaean Provinces in fact extend across the continent and correspond with the Tropical Zone and Eremaean Zone of Burbidge (1960). Their species can be expected to have a trans-Australian distribution. The Southwestern Province is isolated by 1000 miles from any comparable area in the east and is generally believed to contain a high proportion of endemic species.

Discussing the data first on a purely Western Australian basis, it will be seen that only 43 species are known to occur throughout the state, while a further 22 have a northern and southern distribution. The Southwestern Province has by far the richest flora, two-thirds of the total. One-fifth of the Southwestern species occurs also in the Eremaea. The Northern flora is surprisingly small but this may only be due to lack of knowledge and incomplete collecting. Seventy-nine per cent of the Southwestern flora is restricted to that Province, seventy-seven per cent in the case of the Northern, and only forty-five per cent in the case of the Eremaean.

The concept of Botanical Provinces, on which this analysis has been based, is of course purely subjective and there may be those who doubt the reality of it. In cold fact it will be clear that concentrations of species can be expected in the higher rainfall areas of the extreme north and south-west. Arbitrary provincial boundaries based on bioclimatic lines or on plant communities are a convenient means of giving expression to this, and are found to be effective in that 77 per cent of the northern flora and 79 per cent of the southwestern are confined within the chosen provincial boundaries.

The above data do not afford an estimate of true endemism in the Southwestern Province since many species listed as Southwestern on the ground that they do not enter the Eremaea are in fact found elsewhere in Temperate Australia. Further data on species distribution was therefore sought by consulting the authors cited in the References. The wider distribution of the West Australian species thus obtained is given in Table 1, where *Endemic* means confined to Western Australia, *E/Aust.* means occurring in Eastern Australia, *A/Asia* means extending to New Guinea, New Caledonia and New Zealand, and *Cosmo* (cosmopolitan) means having any wider distribution than Australasia.

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Table 1

Wider distribution of Western Australian plant species

	Endemic	E/Aust.	A/Asia	Cosmo.	Total
Provincial Distribution—					
Northern only	355	610	72	80	1117
Northern and Eremaean	64	167	12	20	263
Northern and Southern	11	34	10	10	65
Total N.P.	430	811	94	110	1445
Eremaean only	532	259	11	9	811
Northern and Eremaean	64	167	12	20	263
Southwestern and Eremaean	519	177	5	4	705
All Provinces	7	25	5	6	43
Total E.P.	1122	628	33	39	1822
Southwestern only	2472	280	61	28	2841
Southwestern and Eremaean	519	177	5	4	705
Northern and Southern	11	34	10	10	65
Total S.W.P.	3002	491	76	42	3611

From Table 1 the following percentages of endemism can be calculated:

	%
Northern Province:	
whole northern flora	30
plants solely northern	32
Eremaean Province:	
whole eremaean flora	62
plants solely eremaean	66
Southwestern Province:	
whole southwest flora	86
plants solely southwestern	87

It is to be expected that most species of northern Australia range across the continent, and the proportion confined to the Kimberley District of Western Australia is on the other hand unexpectedly large and it is hard to know whether this conclusion is affected by inadequate information. The southwestern flora, as expected, gives a very high figure and it becomes clear that it is effectively distinct not only from that of the other provinces within Western Australia but from that of South-eastern Australia as well. The reasons for this state of affairs are being discussed in another paper.

It is of interest to compare similar figures given by East in 1912:

> "A consideration of the data at present available for the whole state seems to justify the following estimate of the species more or less restricted to each division and constituting the present flora of the state:—
>
> > South-west division 2,239 species, of which 2,013 are endemic; Eremian or central division, 706 species of which 614 are endemic; north or Kimberley division, 1,221 species of which 780 are endemic. Totals 4,166 species of which 3,407 are endemic."

The proportions are much the same but the totals have risen since 1912, showing the advance in botanical knowledge in half a century. In other respects there has been less progress, as witness this further quotation from East which speaks for itself:

> "It is a matter of great regret that successive Governments have so long neglected to develop the scientific knowledge of the flora of the state. All the other states have compiled and published floras, but that for Western Australia has yet to be written."

Numerical data on certain important families and genera follow.

For assistance in preparing this paper the author is indebted to Mrs. P. Fairall and to Geh Thuan Hsien, who searched the literature mentioned.

Data on selected families

E. Endemic species
O. Others
% Percent endemism

		Northern:	Eremaean:	Southwestern:
Chenopodiaceae:	E.	5	27	14
	O.	16	53	20
	%	24	34	41
Compositae:	E.	13	83	102
	O.	49	94	78
	%	21	47	57
Euphorbiaceae:	E.	15	18	35
	O.	34	17	11
	%	33	52	76
Gramineae:	E.	77	26	30
	O.	96	80	56
	%	45	25	35
Liliaceae:	E.	4	16	77
	O.	7	14	18
	%	36	54	81
Mimosaceae:	E.	27	96	158
	O.	49	29	10
	%	35	77	94
Orchidaceae:	E.	—	4	101
	O.	—	6	42
	%	0	40	70
Papilionaceae:	E.	27	97	290
	O.	78	41	25
	%	26	70	92

Data on selected genera

		Northern:	Eremaean:	Southwestern:
Acacia:	E.	24	95	156
	O.	46	31	12
	%	34	76	94
Boronia:	E.	1	6	28
	O.	2	1	2
	%	33	86	93

Daviesia:

	Northern:	Eremaean:	Southwestern:
E.	2	15	40
O.	1	1	4
%	67	94	91

Drosera:

	Northern:	Eremaean:	Southwestern:
E.	1	3	34
O.	3	2	2
%	25	60	94

Eremophila:

	Northern:	Eremaean:	Southwestern:
E.	1	51	15
O.	3	18	6
%	25	84	72

Eucalyptus:

	Northern:	Eremaean:	Southwestern:
E.	12	43	65
O.	27	19	9
%	31	69	88

Goodenia:

	Northern:	Eremaean:	Southwestern:
E.	5	23	23
O.	10	8	7
%	33	74	77

Helipterum:

	Northern:	Eremaean:	Southwestern:
E.	2	19	10
O.	1	17	10
%	67	53	50

Leucopogon:

	Northern:	Eremaean:	Southwestern:
E.	—	10	97
O.	—	—	4
%	—	100	96

Pimelea:

	Northern	Eremaean:	Southwestern:
E.	—	14	24
O.	5	3	3
%	—	82	90

Stylidium:

	Northern:	Eremaean:	Southwestern:
E.	2	14	80
O.	10	—	5
%	17	100	94

Thysanotus:

	Northern:	Eremaean:	Southwestern:
E.	—	1	20
O.	2	1	3
%	O	50	87

Summation of genera cited

Genera	Northern Province		Eremaean Province		Southwestern Province	
	E.	O.	E.	O.	E.	O.
Acacia	24	46	95	31	156	12
Boronia	1	2	6	1	28	2
Daviesia	2	1	15	1	40	4
Drosera	1	3	3	2	34	2
Eremophila	1	3	51	18	15	6
Eucalyptus	12	27	43	19	65	9
Goodenia	5	10	23	8	23	7
Helipterum	2	1	19	17	10	10
Leucopogon	—	—	10	—	97	4
Pimelea	—	5	14	3	24	3
Stylidium	2	10	14	—	80	5
Thysanotus	—	2	1	1	20	3
TOTALS	50	110	294	101	592	67
% Endemism	32		75		90	

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6.—Conodont and fish remains from the Gneudna Formation, Carnarvon Basin, Western Australia

by George Seddon*

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Abstract

Eight species of conodont and fish remains which include dipnoan palatal plates are described from the Gneudna Formation, Carnarvon Basin, Western Australia. The evidence for age determination and correlation with the Canning Basin is reviewed; with the conclusion that the Gneudna Formation probably represents a relatively short interval of time at the Middle/Late Devonian boundary, and is correlative with a part of the Sadler Formation in the Canning Basin.

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Introduction: the problem

The Devonian fauna from the Carnarvon Basin and its supposed correlatives in the Canning (Fitzroy) Basin are strikingly different in two respects: the Gneudna Formation is rich in individuals but consistently poor in species, whereas the faunas of the Sadler, Gogo and Virgin Hills Formations are richly varied. Moreover, the taxonomic units do not correspond; in fact, of the 18 species that have been named from the Gneudna Formation, only one (*Spinatrypa aspera prideri* (Coleman)) has hitherto been recorded without reservation from the Canning Basin. Most of the species and subspecies described from the Gneudna Formation are endemic to it ("endemic" here equals: recorded only from that formation), as follows:

1. *Nautiloids* (Collins, 1966)

Bulletoceras variabile Collins, with 19 variants. Endemic

Bulletoceras radiatum Collins, with 19 variants. Endemic

These two species belong to the same phylogenetic lineage, and there are transitional forms. The former dominates the lower, and the latter, the upper part of the formation.

Michelinoceras sp. c Collins (a single fragment)

Both *genera* are present in the Canning Basin, and *Bulletoceras* is not known outside Western Australia.

2. *Ostracods* (Jones, 1962)

Cryptophyllus sp. a Jones

This species has been doubtfully recorded from the Frome Rocks Well No. 2, in the Canning Basin, from the *Avonia proteus* zone of Famennian age, but not from the Frasnian formations of the Canning Basin. The genus is cosmopolitan.

3. *Corals* (Hill, 1954)

Disphyllum virgatum (Hinde) var. *variabile* Hill

The *variety* is endemic; the species is cosmopolitan, and is characteristic of the Givetian and Frasnian in Europe. *D. virgatum* var. *densum* Hill is recorded from the Pillara Limestone, Canning Basin.

Hexagonaria gneudnensis Hill. Endemic; closely related to *H. brevilamellata* (Hill) from the basal parts of the Pillara Limestone.

Thamnopora cf *polyforata* (Schlotheim).

T. polyforata s.s. is cosmopolitan and is characteristic of the Upper Givetian and lower Frasnian of Belgium. Neither the species nor the compared species has been recorded from the Canning Basin.

Alveolites caudatus Hill Endemic

4. *Brachiopods* (Coleman, 1951)

Spinatrypa aspera prideri (Coleman): present in the Canning Basin "at Sadler Ridge in the Upper Frasnian *torrida* zone, and probably in the Upper Famennian *proteus* zone in the Geikie Gap area" (Veevers, 1959b, p.20).

(Glenister, 1956)

Austrospirifer variabilis Glenister	Endemic
Cyrtospirifer minilyaensis Glenister	Endemic
Cyrtospirifer australis Glenister	Endemic
Cyrtospirifer gneudnaensis Glenister	Endemic
Cyrtospirifer brevicardinis Glenister	Endemic

Glenister made no comparison between these and other members of the genus.

(Veevers, 1959a, b)

Productella occidua Veevers	Endemic?
Camarotoechia puteana Veevers	Endemic

closely related to *C. congregata* from the upper Givetian and lower Frasnian of New York State.

Spiriferidae gen. et sp. ind.	Endemic

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cf *Ladjia saltica* Veevers. *L. saltica* Veevers ss. is the name bearer of a zone, which Veevers considers to be mid-Frasnian, in the Canning Basin.

5. *Spores* (Balme, 1960)

Balme described 8 species, three of which are new, from the Pelican Hill bore, from sediments correlated with the Gneudna Formation. The endemic species, especially *Geminospora lemurata* are 'overwhelmingly the most abundant.' (p.5). The remaining species . . . can be closely matched with forms occurring in the Givetian and Frasnian deposits in Russia, West Europe or North America' (p.9). But he notes 'the complete dissimilarity from rich Famennian assemblages known from many localities in the Fitzroy Basin' (p.9). There is no account of Frasnian assemblages from the Canning Basin.

Conclusion. Although the Gneudna species are often closely related to species from the Devonian of the Kimberley region, they are nevertheless distinct, and there has hitherto been only one unequivocal claim to taxonomic identity. Others may be established, and further work should be directed towards testing the *tentative* claims. For example, Veevers (1959b, p.26) notes a possible (single specimen) occurrence of *Productella occidua* from the Sadler Formation. The present author, in company with the three Honours students from the University of Western Australia, found a thin band of oncoceratid nautiloids about 30 ft. below the top of the formation at the type locality. These may be referable to *Clavigeroceras suzanni* Collins, described from a mid-Frasnian section of the Virgin Hills Formation (Hosemann, p.133 in Alcock, Hosemann and Read, 1966). Veevers (1959b, p.30) records three specimens of cf. *Ladjia saltica* Veevers from the Gneudna Formation. The Honours students referred to above failed to find further specimens (Hosemann, p.132 in Alcock, Hosemann and Read, 1966).

However it is clear from the data presented above that additional work on the Gneudna fauna over the years has given a cumulative emphasis to its taxonomic distinctness rather than the reverse, and this requires explanation.

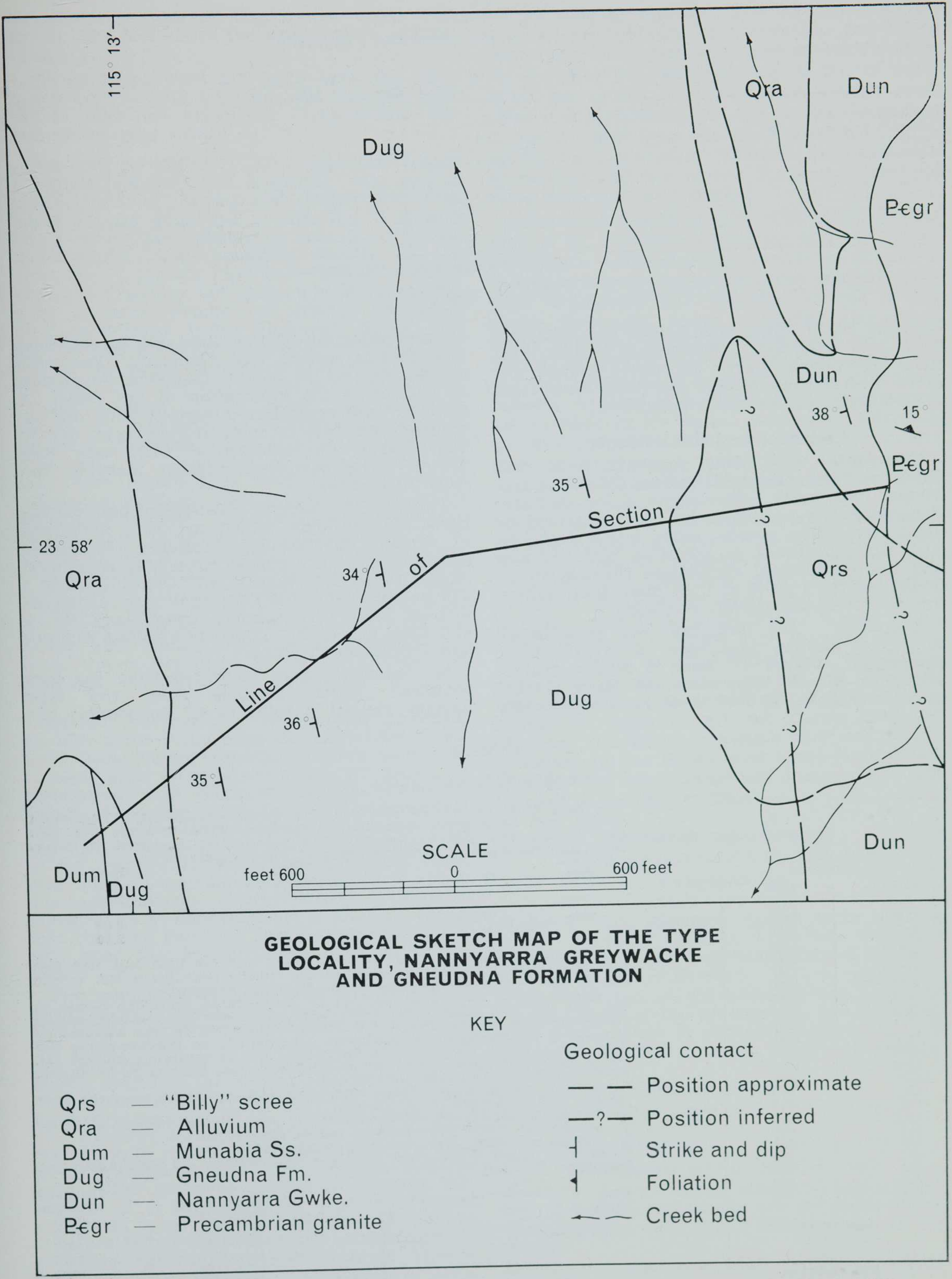
Hill (1954, p.8) provisionally correlated the Gneudna Formation with the lower part of the Pillara Limestone of Givetian age and concluded that "differences in species between the two limestones may be due to differences in province between the Carnarvon and Kimberley regions". Two things can be said about this supposition. The first is that these two regions do not today represent two marine provinces; they both fall within the Dampierian Province of Hedley, 1926. The second is that even if they did (if, for instance, we were comparing the shelf fauna off Broome with that from Cockburn Sound), there would be a high degree of overlap, with many common species. For example, of 99 species of foraminifera recorded from Western Australia, 31 show a preference for tropical and subtropical waters and 18 for temperate waters, but the other half show little latitudinal preference (Betjeman, 1965, p.49-52). Of some 290 species of echinoderms recorded from the Dampierian province, only 40 are not also found along the more southern coasts (Clark, 1946, p. 467). Ekman (1953, p.202) adds palaeontological data, and concludes: "we may say with reference to the sea-urchins, and in all probability also the greater part of the South Australian shelf fauna, a weak affinity with the rest of the temperate southern fauna and a considerably closer affinity with the tropical fauna was a characteristic feature at all geological periods from the Cretaceous inclusive".

Poverty of the Gneudna fauna. Balme (1960, p.1) writes of "Microfloras rich in individuals but poor in species." Collins (1966, p.iii) notes that "the rich and diverse Fitzroy Basin fauna includes 17 orthocerid, 10 discosorid, 9 oncocerid and 4 bactritid spp. referable to 18 genera. In contrast, the numerous representatives from the Carnarvon Basin comprise only 2 discosorid and 1 orthocerid species referable to 2 genera." The brachiopod and coral assemblages are also rich in individuals and poor in species. Collins (1966, p.26) concludes that "the rich and varied nautiloid and bactritid assemblages of the Fitzroy Basin are a reflection of the great variety of ecological niches provided by a large reef complex. Similarly, the large numbers of few species in the Gneudna Formation is a reflection of the rather uniform environment of the open shelf." This may very well be the case, but ecological comparisons have no value until correlation is firm. This is apparent if we compare the Gneudna nautiloid faunule, not with the "rich and diverse Fitzroy Basin fauna" but with that of the Sadler Formation, from which Collins reports only six species of nautiloid and two bactritids (p.14). The age of the Gneudna Formation is relevant to the apparent poverty of the fauna in two ways: the first is that it may represent a relatively short interval of time: much of the apparent richness of the

Table 1

Conodonts from the Gneudna Formation

	G 8–9	G 10	G 12	G 12c	G 13	G 14	G 14+
Angulodus sp.		1					
Bryantodus. sp.	1						
Hindeodella subtilis		10		6			
Icriodus nodosus		3	1	8	4		1
Ozarkodina immersa		1			2		
Pelekysgnathus ? sp.	1						
Polygnathus pennatus		4		9	10	1	
Synprioniodina sp. cf. *S. prona?*		1					
Synprioniodina sp. cf. *S. prona*					3		



GEOLOGICAL SKETCH MAP OF THE TYPE LOCALITY, NANNYARRA GREYWACKE AND GNEUDNA FORMATION

Figure 1.—Location of the sampled section. Map redrawn from Alcock, Hosemann and Read (1966).

Table 2

Fish remains from the Gneudna Formation

	4	7+	8p	8–9	9	9c	10	12	12c	13	13e	14	14+	15	cc12	cc14
Fish teeth, type a										+	+					
Fish teeth, type b	+			A			+									
Fish teeth, type c						+				+						
Conical teeth, type d				A	A		A	A	A	A			+	+	+	
Fish teeth, type e			+	+										+		
Rhomboid scales				A	A			A	A	A	A					
Fin scales (?)					A					A						
Bone fragments				+	A			+		A			+	+		+
Dipterus plates		+								+						

Notes : + = present in sample ; A = very abundant.

Nos. 4–15 are from the type locality of the Gneudna Formation.

. cc12 and cc13 are cores from Cape Cuvier 1 at 1,423 ft. and 1,480 ft.

Canning Basin fauna comes from the relatively condensed sequences. The second is that, with some exceptions, Upper Devonian faunas are more diverse than Middle Devonian ones (this is strikingly true of the conodonts).

Conodont and fish evidence

Conodonts were first reported from the Gneudna Formation by Glenister (McWhae and others, 1958, p.43). Specimens of *Icriodus* and *Polygnathus* were noted, but not described or illustrated. The present study was undertaken with the expectation of achieving both regional and intercontinental correlation through conodonts, but the results do little more than underline the problems already discussed.

Sampling. The formation was sampled at the type locality south-east of Williambury Homestead (Figure 1) along a section plane-tabled by Alcock, Hosemann and Read (1966). 28 bulk samples of 5-10 lb of rock were taken at approximately 50-foot intervals across some 1400 feet of section (see Table 3). The most distinctive feature of the Gneudna Formation in outcrop is the alternation of low ridges of medium-hard crystalline limestone with shallow troughs underlain by more friable rocks, mostly quartzwacke and calcarenite, with some siltstone. The samples represent most of the ridge limestones.

Three of the samples consisted of bulk collections of nautiloids, which are very abundant at certain stratigraphic horizons. (Nautiloids and conodonts are almost invariably associated in the Upper Devonian of the Canning Basin.) The samples from the type locality were supplemented by 6 core samples from Quail No. 1 and Cape Cuvier No. 1, drilled by West Australian Petroleum Pty. Ltd.

No conodonts were recovered from the core samples. Seven samples from the type locality yielded a total of 67 conodonts; the

Table 3

Locality data and notes

1	2
Munabia Sandstone	
G16a+	1820
G16a	1810
G15b	1645
G15	1590
G14+	1502
G14	1480
G13+	1345
G13	1326
G12c	1245
G12	1188
G11	1128
G10c	1085
G10	1052
G9g	1016
G9c	968
G9	925
G8	807
G7g	762
G7	656
G6	551
G5	495
G4	466
G3a	442
G2	408
Nannyarra Greywacke	
Precambrian	

A. The base and the top of the Nanyarra Greywacke-Gneudna Formation section may be located on aerial photographs, Winning Pool, W.A. 837, run 17, 5242 and 5243 by the following coordinates, measured in inches from the western and northern edges of the photographs.

		Top	Base
5242	W - E	2.06	2.96
	N - S	3.34	2.84
5243	W - E	5.78	6.68
	N - S	3.30	2.80

The line of section from the base bears 262° for 1,550 feet (100 feet past the small valley at the crest of the ridge): then bears 240° to the end of the section at the base of the Munabia Sandstone.

Bench marks have been painted on outcropping limestone bands at 495, 550, 660, 800, 1,330, 1,480, 1,530, 1,600 and 1,755 feet stratigraphically above the base of the section. A uniform dip of 35° W was assumed in computing the stratigraphic thickness. The column at the left shows the field no's (1) and the height in feet above the Precambrian contact (2). For a rock description of the sampled intervals, see Hosemann, in Alcock, Read and Hosemann, 1966, pp. 141-144.

B. In addition to the above, three bulk nautiloid collections from the type locality were processed for conodonts.
1. Sample no. 58048: 460-470 feet above the Precambrian contact, about G4
2. Sample no. 58067: 792-1020 feet, about G8-G9
3. Sample no. 58085: 1795-1810 feet, about G16A

C. Cores from Quail 1 and Cape Cuvier 1 (by courtesy of West Australian Petroleum Pty. Ltd.)

Well	Core No.	Interval Cored	Depth of Sample
Quail 1.	15	9163-9173	9168
	16	9741-9751	9742
Cape Cuvier 1.	12	1411-1416	1413
	13	1471-1476	1475
	14	1476-1484	1480
	15	1489-1494	1493

stratigraphic interval represented runs from 807 to 1502 feet above the Precambrian contact (Table 1).

Fish remains were recovered from the Cape Cuvier core at 1413 feet and 1480 feet and from 466 to 1590 feet above the Precambrian contact at the type locality.

Age and correlation. The conodont faunule is simple, consisting of 8 species, only two of which, *Icriodus nodosus* and *Polygnathus pennatus* s.l. are abundant. Although it is certainly either late Givetian or Frasnian, it is not clear which. The conodont species in the Gneudna Formation have been widely recorded from the Frasnian, but commonly in association with a large number of highly restricted, characteristically Upper Devonian forms (the ancyro- and palmatolepid-groups). The simplicity of the fauna is more characteristic of the Givetian, but Givetian indices are also lacking.

The dipnoan plates from the Gneudna Formation are probably referable to *Dipterus digitatus* Eastman, first described from the State Quarry Limestone of Iowa, which has long been regarded as basal Upper Devonian (Cooper and others, 1942, p.1783), chiefly on its brachiopod faunule. The State Quarry Limestone was sampled in detail for conodonts by A. R. Ormiston and A. B. Shaw in 1965. Faunas are characterized by *Icriodus nodosus, Polygnathus decorosus* s.l. (roughly synonymous with *P. pennatus* s.l.), and *Spathognathodus insitus* (Stauffer). The latter species is known only from the Lower and Middle *Polygnathus asymmetricus* zone, Upper Devonian, *to Iα* in Alberta and Montana (Glenister and Rexroad, 1968, pp.6-12).

Icriodus nodosus and *Polygnathus decorosus* s.l. also occur throughout the underlying Givetian) Cedar Valley Limestone in Iowa, as they do in many other Givetian sequences, but usually in association with distinctive Middle Devonian forms. However, in the Coralville (uppermost) Member of the Cedar Valley Limestone, these two species dominate the conodont faunule, and in the *Straparollus* zone, the uppermost biotic unit of the Coralville Member, there is also a dipnoan, *Dipterus calvini*, which is directly ancestral to *D. digitatus*. It is probable therefore that the Gneudna fauna indicates an age very near the Middle/Upper Devonian boundary.

The conclusion that the Gneudna Formation is of latest Givetian and/or earliest Frasnian (lower to Iα) age returns to that of Hill (1954), but differs from that of Veevers (1959b, p.23) who estimates that the lower half is "probably Middle Frasnian, the upper half probably upper Frasnian". However this estimate arises from Veevers' correlation of the Gneudna Formation with the *saltica* and *torrida* zones of the Sadler Formation in the Canning Basin, which he considers to be middle and upper Frasnian respectively. The apparent conflict of evidence disappears if it is recognized that the Sadler Formation is not middle and upper Frasnian; it rather is latest Givetian and early Frasnian, and does not range beyond *to Iα*. This is clear both from Glenister and Klapper's (1966, text-fig.2) conodont work, and from extensive re-sampling by myself. The conodont faunule can be referred to internationally recognized zones, and there can be no serious doubts about this correlation. The brachiopods, on the other hand, are mostly endemic at the specific level. Once it is recognized that the Sadler Formation is not younger than earliest Frasnian, the evidence for correlation between the Gneudna Formation and the Sadler Formation becomes more coherent, as follows:

Spinatrypa aspera prideri (Coleman) is common to the Gneudna Formation and the Sadler Formation. The probable occurrence of *Ladjia saltica* in the Gneudna Formation and the possible occurrence of *Productella occidua* in the Sadler Formation tends to confirm the correlation. Both the Pillara Formation and the Sadler Formation are in part late Givetian, and thus the coral evidence is consistent. The conodonts *Icriodus nodosus* and *Polygnathus pennatus* s.l. are common in the Sadler Formation, although the Sadler Formation also has the *to Iα* indices such as *Ancyrodella rotundiloba* in its upper part. The Gneudna conodonts, on the other hand, show no change over some 700 feet of section, and it is probable that the formation records a relatively short time interval, despite the stratigraphic thickness. This would then be a partial explanation both of the limited variety of the Gneudna fauna, and of the failure to match closely the total Sadler fauna, which would represent a longer time interval. However, it should be emphasized that the differences remain striking: one not yet noted is that although nautiloids are plentiful in all three formations goniatites are not known from the Gneudna Formation, although they are superabundant in the Sadler and Gogo Formations. This and the other differences discussed are still in need of credible explanation.

Systematic palaeontology

Genus ANGULODUS Huddle, 1934

Angulodus sp.

Plate 1, figure 7

Remarks: The specimen figured lacks a main cusp. In other respects it accords well with Huddle's (1968, p.8) redescription of *A. pergracilis* (Ulrich & Bassler).

The denticles of the posterior bar alternate in size: those of the anterior bar are subequal. The anterior bar is deflected downwards and inwards. The bar is heavy, but is not laterally compressed.

Locality: one specimen, from G 13.

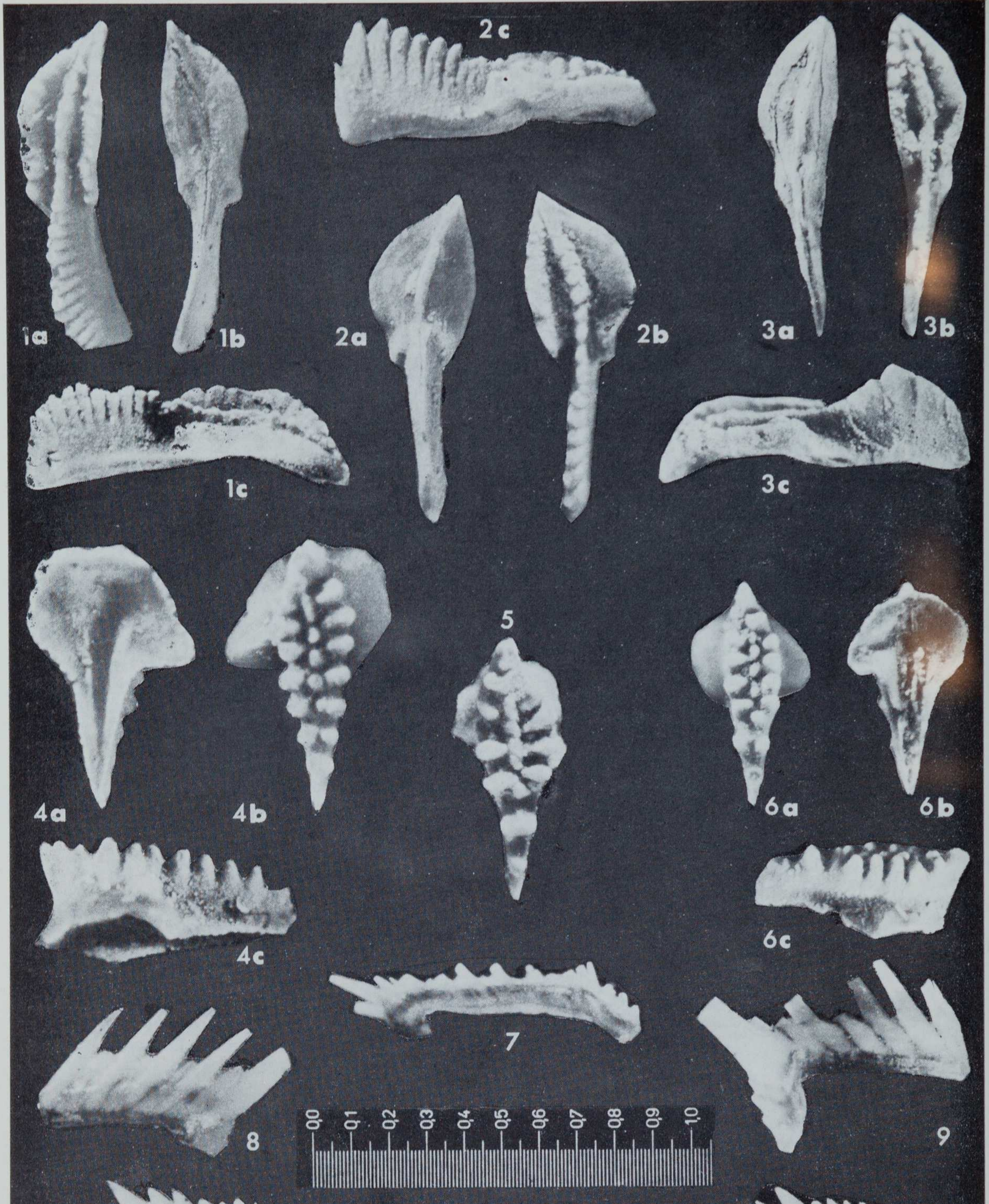
Repository: figured specimen (UWA 62136).

Genus HINDEODELLA Bassler, 1925

Hindeodella subtilis Bassler, 1925

Remarks: Several almost complete, and a number of broken, specimens are in good accord with Huddle's (1968, p.17) redescription of this species.

Locality: 7 specimens from G 10; fragments in G 12c.


1a
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9
10
11
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0,9
1,0

Genus ICRIODUS Branson & Mehl, 1938

Icriodus nodosus (Huddle), 1934

Plate 1, figures 4a, b, c; 5, 6a, b, c

Remarks: As Glenister and Klapper note (1966, pp.805-806), *Icriodus symmetricus* and *I. nodosus* cannot at present be discriminated with precision; the margin of the basal cavity is broken in the holotype of *I. nodosus* (Huddle, 1934, Pl. 8, figs. 24, 25). *I. nodosus* s.l. is characterized by a sinus in the margin on the inner side of the posterior expansion of the basal cavity, forming a prominent, anteriorly directed spur. Typical specimens of *I. symmetricus* lack such a spur and sinus; however many specimens of very late Middle Devonian age are transitional between *I. symmetricus* and *I. nodosus* s.l. *I. corniger* Wittekindt also has a spur and sinus, and differs from *I. nodosus* s.l. only in that the basal cavity is produced to a sharp point slightly to the outer side of the posterior end. The specimen illustrated as *I. corniger* Wittekindt by van A. Boogaert (Pl. 1, fig. 6a,b) is transitional to *I corniger*. The specimens from the Gneudna Formation are variable; the large figured specimen (Pl.1, fig. 4a,b,c) has a well developed lateral spur which bears a low ridge of fused nodes on its upper surface. In other specimens (not illustrated) the spur is only weakly developed, and these might be referred to *I. symmetricus*. The lateral denticles in all specimens are lachryform; they tend to alternate with the denticles of the middle row, which are laterally compressed. In a few specimens the denticles of the middle row are fused (Pl. 1, fig.5).

Age: I. nodosus s.l. ranges through the Middle Devonian into the lowermost Upper Devonian.

Locality: 17 specimens were recovered from 5 samples from 1052 to 1502 feet (G 10, G 12, G 12c, G 13 G 14+) above the Precambrian contact at the type locality of the Gneudna Formation.

Repository: Figured specimens (UWA 62133, 34. 35).

Genus OZARKODINA Branson & Mehl, 1933

Ozarkodina immersa (Hinde), 1879

Plate 1, figures 10, 11

Remarks: Müller and Clark (1967, p.915) put *O. elegans* Stauffer in synonymy with *O. immersa* by direct comparison with Hinde's type specimen. Note that the specimen figured as Plate 1, figure 11 has two "main" denticles.

Age: Givetian-Frasnian.

Locality: 4 specimens were recovered from 2 samples (G 10, G 13) at the type locality.

Repository: Figured specimens (UWA 62139, 40).

Genus PELEKYSGNATHUS Thomas, 1949

Pelekysgnathus ? sp.

Remarks: A single incomplete specimen was recovered from a nautiloid from Gud 9, approximately 1,000 feet above the base of the Precambrian contact at the type locality. The specimen consists of a single row of denticles with a large posterior denticle, posteriorly inclined. The anterior part is missing. Seen from above and in side view, this specimen would be referred without hesitation to *Pelekysgnathus,* but the basal cavity is unusual: it flares under the terminal denticle, as with *Icriodus* and *Pelekysgnathus,* but instead of tapering towards the anterior end, the flared margins meet abruptly a little anterior to the position of the terminal denticle.

Genus POLYGNATHUS Hinde, 1879

Polygnathus pennatus Hinde, 1879

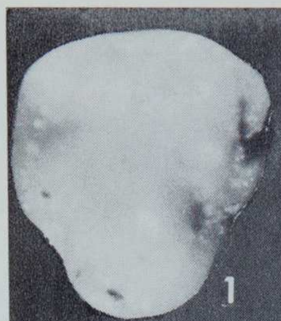
Plate 1, figures 1a, b, c; 2a, b, c; 3a, b, c

Remarks: Specimens such as those illustrated are familiar to all conodont workers who have examined Givetian-Frasnian faunas. The problem is what to call them. The specimen figured in Plate 1, figure 1a,b,c is typical Gneudna specimen: the high free blade is slightly shorter than the platform, and the basal cavity is about half-way between the mid-point and the anterior margin of the platform. The platform is weakly ribbed. The other two figured specimens are extreme variants. The specimen of Plate 1, figure 3a,b,c is strongly sigmoidal in side view, has a high free blade with fused denticles and a narrow platform with strongly upturned margins and little surface ornament. Specimens such as this are often referred to *P. foliatus* Bryant (e.g., Müller and Clark, 1967, Pl. 115, fig. 4). The specimen of Pl. 1, fig. 2a,b,c resembles *P. eiflia* Bischoff and Ziegler in outline, especially in the flared outer platform margin and anterior constriction, although the platform lacks the nodes and adcarinal ridges of that species. Wittekindt (1966, p.633 redefined *P. eiflia* such that the adcarinal ridges, although characteristic, are not to be considered diagnostic *of P. eiflia.* Thus my specimen might be referred to *P. eiflia,* if the smoothness of the platform be admitted as intra-specific variation.

However, the Gneudna specimens cannot be sorted into three groups and I prefer to regard them as representing a single, rather variable species. *P. pennatus* is the senior species concept, and they are therefore provisionally included in it.

Age: the loosely interpreted *P. foliatus-P. pennatus* group range through the upper Givetian into the Frasnian.

Plate 1 (facing page) Specimens from the type locality of the Gneudna Formation, Carnarvon Basin, Western Australia. All figures are un-retouched photographs. The platform species are coated with ammonium chloride, but the bars and blades (figs. 7-11) are uncoated. Figures 1, 2, 3 and 7 are x40. Figures 4, 5, 6, 8, 9, 10 and 11 are x60, and the bar scale, which represents 1 mm, applies only to these. Figures 1-3.—*Polygnathus pennatus* Hinde. (UWA 62130, 62131, 62132). Figure 1 is a typical specimen; figure 2 has a broader and unornamented platform; figure 3 is a "*P. foliata*" type. (All specimens from G13). Figures 4-6.—*Icriodus nodosus* (Huddle). (UWA 62133, 62134, 62135). Figure 4 has a well developed lateral spur with a prominent node or ridge on the upper surface. In Figure 5 the mid-row of denticles is clearly expressed only in the posterior half, where it is fused into a longitudinal ridge. (G 13, G 10, G 13). Figure 7.—*Angulodus* sp. (UWA 62136; G 13). Figure 8.—*Synprioniodina* sp. cf. *S. prona* (Huddle)? (UWA 62137; G 13). The anticusp is broken off this specimen). Figure 9.—*Synprioniodina* sp. cf. *S. prona* (Huddle).—(UWA 62138; G 13). Figures 10 and 11 —*Ozarkodina immersa* (Hinde). UWA 62139, 62140; G 13).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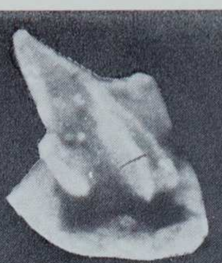
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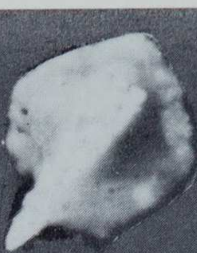
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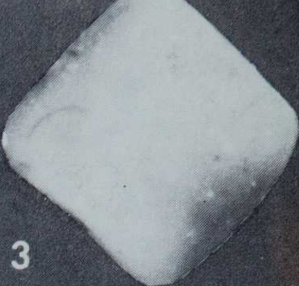
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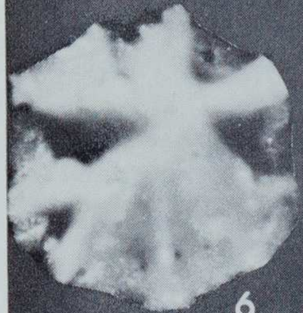
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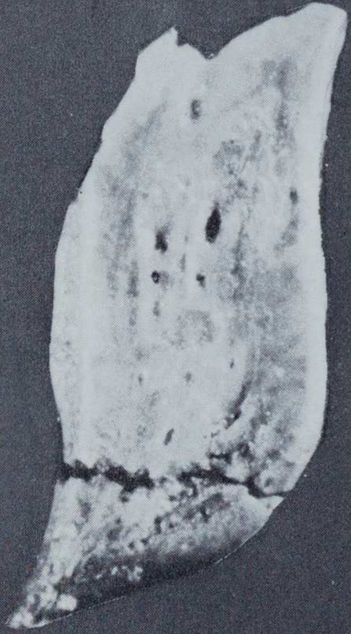
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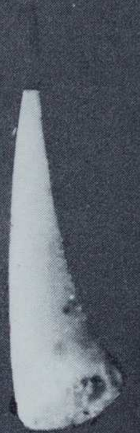
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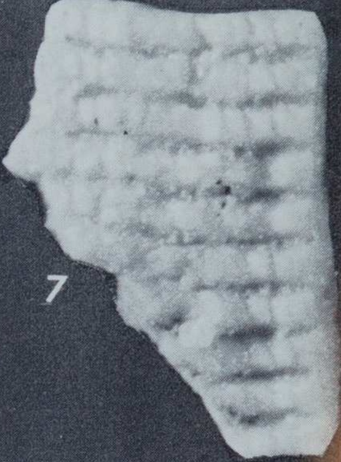
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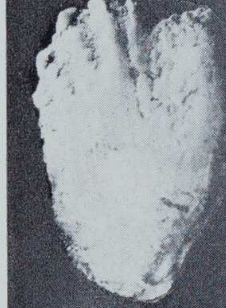
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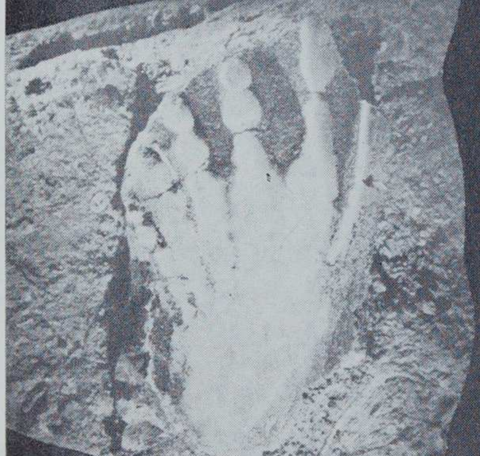
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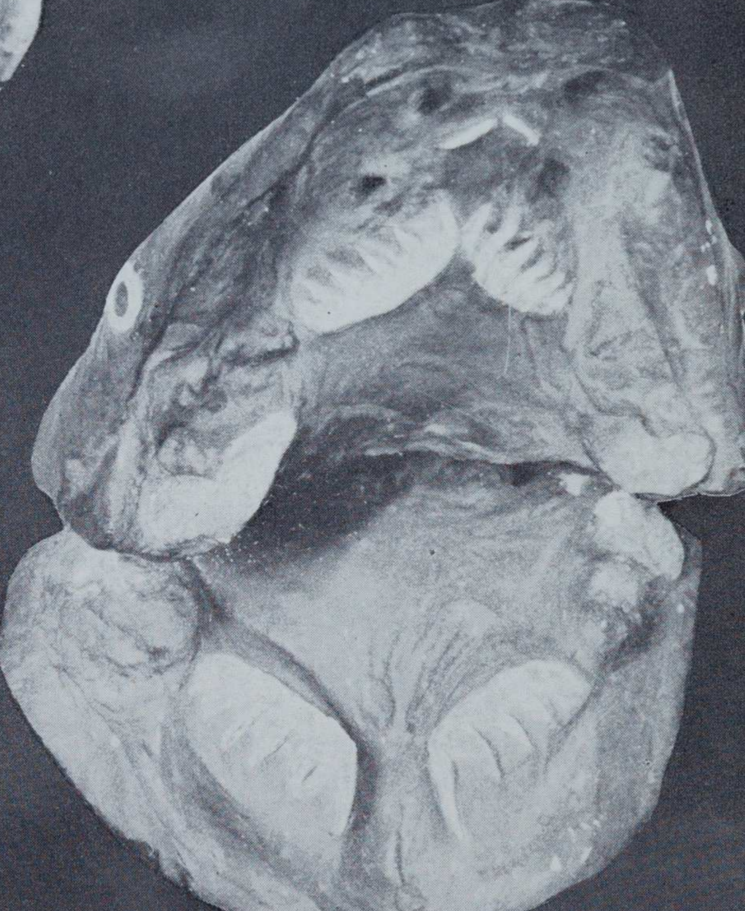
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Locality: 24 specimens were recovered from 4 samples from 1052 to 1480 feet (G 10, G 12c, G 13, G 14) above the Precambrian contact at the type locality of the Gneudna Formation.

Repository: Figured specimens (UWA 62130, 31, 32).

Genus SYNPRIONIODINA Bassler, 1925

Synprioniodina sp. cf. *S. prona* (Huddle), 1934

Plate 1, figure 8 ?, figure 9

Remarks: Huddle (1968) distinguishes *Neoprioniodus* and *Synprioniodina* on the denticulation of the anticusp. '*Neoprioniodus* is distinguished by its non-denticulate anticusp' (p.45) but 'Anticusp not denticulated in most species, but some species have a few denticles' (p.25). The specimen figured here is a borderline case, as the anticusp bears three small, fused denticles. In the specimen figured as *S.* sp. cf. *S. prona* ? (Pl. 1, fig. 8) the anticusp is broken and incomplete. It differs visibly from *S.* sp. cf. *S. prona* only in that the large denticles are wider spaced, with 'germ denticles' between them. The angle between the bar and anticusp cannot be determined.

Localiy: 4 specimens from 2 samples (G 10, G 13).

Repository: Figured specimens (UWA 62137, 38).

Class: OSTEICHTHYES

Sub Class: CHOANICHTHYES

Order: Dipnoi

Family: Dipteridae

Dipterus sp. cf. *D. digitatus* Eastman, 1908

Plate 2, figure 9

1908 *Dipterus digitatus* sp. nov.—Eastman, p. 221-222, Pl. 2, fig. 6; Pl. 7, figs. 16-25.

Orientation: A plaster cast of the head of the Queensland lungfish, *Epiceratodus forsteri* (Pl. 2, fig. 10) shows the orientattion of the dental batteries. The upper plates are the palatal plates, and the lower ones, the mandibular plates. The mandibular plates of most Devonian dipterines are convex, and the palatal plates are flat or slightly concave. The plate illustrated as figure 9 is a presumed right palatal plate: that of figure 8 is a left mandibular plate.

Description: Two specimens have been found, both right palatal plates. The larger of the two (Pl. 2, fig. 9) is 3.5 cms long and 2 cms wide; although extremely well preserved, the margins are broken. The original outline was probably subtriangular. Six costae are preserved; four of these become indistinct at about mid-length. The other two costae fuse at mid-length, and continue as a low, smooth, arcuate ridge to the posterior edge. The costae are tuberculate or noded; the nodes are fused except towards the anterior margin, where they are distinct and well-rounded. The nodes of the most strongly developed costa (second from the inner side) are laterally compressed. The spacing of the costae increases from the outer to the inner margin.

The smaller specimen (2 cms long, 0.9 cms wide) is equally well preserved, but slightly less complete. It differs from the figured specimen only in that the costae just fail to reach the mid-point of the plate, and that there is a well developed sinus between the fused, inner costae and the group of outer costae. Both these characters are shown in the topotypic specimen (Pl. 2, fig. 8) from the State Quarry Limestone of Iowa, but these features were judged to be minor intraspecific variation by Eastman, judging from his illustrations of Plate 7, figures 16-25.

Plate 2 (facing page).—Specimens from the type locality of the Gneudna Formation, Carnarvon Basin, Western Australia. All figures are un-retouched photographs. The specimens are coated with ammonium chloride. Figures 1-7 are approximately x45, as is the scale. Figure 1.—Fish tooth; type a (UWA 62141; G 13e). Figure 2.—Fish tooth; type b (UWA 62142; G 10). Figure 3.—Fish tooth; type c (UWA 62143; G 9c). Figure 4.— Fish scale (UWA 62144; G 13). Figure 5.—Conical fish tooth; type d (UWA 62145; G 13). Figure 6.—Fish tooth; type e (UWA 62146; G 8p). Figure 7.—Acanthodian fin scale? (UWA 62147; G 13). Figure 8.—*Dipterus digitatus* Eastman. Left mandibular plate. *Synthetodus* zonule, North Liberty Phase, State Quarry, Johnson Co., Iowa. Basal U. Dev. (C. H. Belanski Collection, W. Aust. Mus. 64.10.5; x 1.4). Figure 9.—*Dipterus* sp. cf. *D. digitatus* Eastman. Right palatal plate (UWA 62148; G 7 +; x 1.4). Figure 10.—*Neoceratodus forsteri*. Plaster cast of Queensland lungfish head showing palatal teeth. (W. Aust. Mus. PIQ05; about 2/3rds natural size).

Remarks: Eastman illustrates two distinct lineages from the Devonian of Iowa. One begins with *D. uddeni* from the Middle Devonian, Cedar Valley Limestone. Two Upper Devonian species from the State Quarry Limestone, *D. mordax* and *D. pectinatus* appear to be derived from it. In all these species the many costae run right to the posterior edge, and there is no inner ridge. The nodes of the costae tend to be en echelon, in that their long axes are at an acute angle to the axis of the costae. The dipterines from the Chemung of Eastern North America are of this type.

The second lineage begins with *D. calvini*, also from the Cedar Valley Limestone (from "the *Euomphalus* bed, about 8 feet below the summit of the Middle Devonian in Muscatine County" Eastman 1908, p.220). This species was founded on a single specimen; it has two early Frasnian derivatives, *D. costatus* and *D. digitatus*. All three species have an anterior ridge, which is more strongly developed in the Frasnian spp., and costae which die out at about mid-length. *D. costatus* is distinctive in that the anterior ridge is separated from the other costae by a marked sinus. Eastman does not give a differential diagnosis for *D. calvini* and *D. digitatus*, which look very similar in his illustrations, except that the mandibular plates and *D. digitatus*, which look very similar in his specimens from the Gneudna Formation are presumed to be palatal plates. They should clearly be referred to the *D. calvini-D. digitatus* lineage and should probably be included in the latter species.

Age: The known range of *D. calvini-D. digitatus* is from the late Givetian to early Frasnian.

Locality: The figured specimen was collected from a thick-bedded, blocky limestone 1345 feet above the Precambrian contact at the type locality (sample no. G 13+, a few yards above G 13; the small specimen, from G 7+).

Repository: UWA 62148.